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A New Species of Early Pleistocene Cotton Rat from the Anza-Borrego Desert of Southern California

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Abstract.—Fossil cotton rats, genus *Sigmodon,* were recovered from the superposed Vallecito-Fish Creek beds of the Palm Spring Fm. in Anza-Borrego State Park, California. *Sigmodon minor* is the common cotton rat species throughout the late Pliocene Layer Cake and Arroyo Seco faunal intervals. A new species, *S. lindsayi,* characterized by large size and a suite of features of the first lower molar, appears first in the early Pleistocene Vallecito Creek faunal interval, extending from collecting zone 53.8 to zone 58.8, from approximately 610 to 305 meters from the top of the sequence. *Sigmodon lindsayi* is replaced in zone 57.8, at about the 366 meter level, by *Sigmodon minor,* but appears once again in zone 58.8, at approximately the 305 meter level, above which it is not recorded. There is no evidence that the two species were sympatric in the Anza-Borrego sequence, but it is likely. The replacement pattern is interpreted as either 1) incorrect stratigraphic assignment of some specimens or 2) the result of competition and possibly habitat modification.

Cotton rats are by far the most commonly recovered small mammals in many deposits of late Pliocene and Pleistocene age throughout the southern United States. Because there are often enough specimens for statistical treatment, and additionally because there is a large body of neontological data from extant species for consultation, cotton rats make ideal subjects for evolutionary and paleoecological study (Martin 1979, 1984, 1986). The occurrence of cotton rats in the Palm Spring Formation of the Anza-Borrego Desert is important, as this is one of the few rock sequences in the United States where cotton rat remains have been recovered in stratigraphically superposed beds that span a considerable amount of time. Consequently, macroevolutionary and macroecological patterns can be documented. This paper represents the results of an initial taxonomic study of the Palm Spring Fm. cotton rat remains, and reports the presence of a new species from the upper, early Pleistocene Vallecito Creek faunal zone. The geology, collecting horizon information, and magnetostratigraphy of the Vallecito-Fish Creek sequence was described by Downs and White (1968) and Opdyke et al. (1977).

The planed and prismatic dentition of cotton rats is more akin in function to that of their northern ecological analogues, the arvicolines, and rather than use the cumbersome cricetine dental terminology of Hershkovitz (1962), we have chosen to use instead the arvicoline terminology of Van der Meulen (1978) for the first lower molar. Homologies are given in Fig. 1. Measurement methods follow Martin (1979) and Czaplewski (1987). Both occlusal and basal lengths are

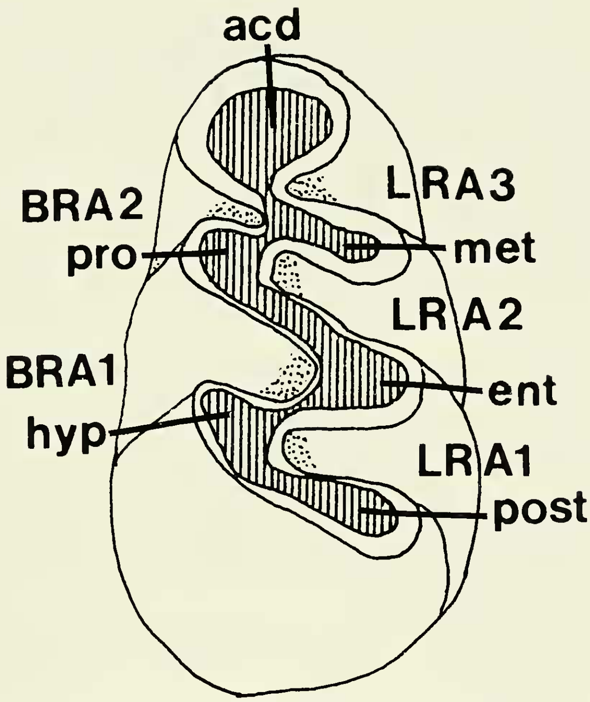

Fig. 1. Topography of a *Sigmodon hispidus* left first lower molar. BRA = buccal reentrant angle, LRA = lingual reentrant angle, acd = anteroconid, pro = protoconid, met = metaconid, hyp = hypoconid, ent = entoconid, post = posterior cingulum or posterolophid. Homologies of reentrant angles to folds, as published by Hershkovitz (1962) and others, are as follows: BRA1 = major fold, BRA2 = first minor fold, LRA1 = second primary fold, LRA2 = first primary fold, LRA3 = first secondary fold.

provided for consistency (see Tomida 1987:103). Abbreviations are as follows: LACM = Los Angeles County Museum, MSU = Michigan State University, L = left, R = right, upper and lower molars (M) indicated by super- and subscript numbers, respectively. The term "zone" as used throughout this paper refers to a specific collecting horizon (level) of Downs and White (1968) in the Vallecito-Fish Creek sediments.

Systematic Paleontology

Order Rodentia Bowdich, 1821

Family Cricetidae Rochebrune, 1883

Sigmodon Say and Ord, 1825

Sigmodon lindsayi, new species

Holotype.—LACM 124161, LM_1, from zone 57.6 (Locality LACM 1114).

Paratypes.—Zone 57.6 (Locality LACM 1114): LACM 124276, LM^2; 124136, RM_3; 124117, RM_1; 3402, LM_3; 124154, RM^1; 124144, RM^1; 124122, LM_1; 124146, RM^1; 124139, LM^3; 124123, LM_1; 124132, LM_3; 124278, LM^2; 124280, LM^2; 124260, RM^3; 124270, RM^2; 124266, LM_2; 124263, RM^2; 124261, RM^2; 124166, RM_3; 124282, RM_2; 124268, RM^2; 124168, RM_2; 124283, LM^2; 124169,

LM^2; 124272, LM^2; 124265, RM^2; 124264, RM^3; 124129, RM^3; 124148, RM_1; 124187, LM^2; 124130, RM^3; 124190, LM^3; 3400, RM_1; 3397, LM_1; 124126, LM_1; 124120, LM_1; 124135, RM^3; 124111, RM_1; 124140, LM^3; 124188, RM^1; 124138, LM^3; 124191, RM_1; 124134, RM^3; 124193, LM_3; 124192, LM_3; 124152, LM^1; 124157, LM^1; 124162, RM_3; 124153, LM^1; 124143, RM^1; 124133, RM^3; 124124, LM_1; 124155, LM^1; 124131, RM^3.

Horizon and type locality.—Collecting zone 57.6 (Locality LACM 1114) of Downs and White (1968), approximately 366–305 meters from top of the Vallecito-Fish Creek sequence, Palm Spring Formation, Anza-Borrego Desert State Park, San Diego Co., California; early Pleistocene (early Irvingtonian land mammal age).

Referred specimens.—The following specimens were also recovered from the Vallecito Creek-Fish Creek sequence of the Palm Spring Formation.

Zone 53.8 (Locality LACM 4963): LACM 122964, RM_1.

Zone 55.5 (Locality LACM 1615): LACM 124242, RM^1; 124238, LM_1; 124251, LM^1-M^3; 124257, LM_3; 124258, LM^2; 124248, part R mandible with M_1-M_2; 124252, L maxillary fragment with M^1-M^2-M^3; 124233, RM^2; 124249, part L mandible with M_1-M_2-M_3; 124234, LM_2; 124259, LM_3; 124235, RM^3; 124236, LM^2; 124241, LM^1; 124240, RM_1.

Zone 55.9 (Locality LACM 1297): LACM 6940, part R mandible with M_2-M_3.

Zone 57.7 (Locality LACM 1461): LACM 124197, part R mandible with M_1-M_2-M_3.

Zone 58.8 (Locality LACM 1114): LACM 3396, RM^1; 7037, RM_2; 3399, LM_3; 3401, RM_2.

Diagnosis.—Size large, teeth hypsodont (Table 1, Fig. 2): anteroconid of M_1 wide, anteroposteriorly flattened, symmetrically extended both labially and lingually, and with an occasional enamel atoll in teeth with little wear; metaconid often bulbous and posteriorly directed; protoconid often triangular; lingual reentrant angle (LRA) 2 deep and anteriorly directed; first lower molar with either three or four well-developed roots.

Etymology.—Named in honor of Everett H. Lindsay, whose research on the correlation of upper Pliocene and Pleistocene North American sediments provides a modern framework for evolutionary studies.

Description.—The following description applies to both the holotype and paratype material. Measurements of the dentition are presented in Table 1.

M_1: The anteroconid is large and, in teeth with moderate wear, anteroposteriorly flattened (Fig. 3). It has both labial and lingual extensions. Reentrant angles are narrow and similar to most other cotton rat species except modern *Sigmodon leucotis,* in which the reentrant angles are wide and the M_1 appears long and narrow. In teeth with little or moderate wear, LRA3 and BRA2 directly abut, with only a thin isthmus of dentine connecting the anteroconid and protoconid. This isthmus may widen in heavily worn teeth. Lingual reentrant angle 2 is often deep and anteriorly extended, where it may nearly touch the enamel wall of BRA2. In specimens from Zone 57.6, the metaconid is bulbous and posteriorly directed, and the protoconid may appear triangular in outline. An enamel atoll is present in the anteroconid of two of eight specimens, lying just above the junction of BRA2 and LRA3. The atoll is lost with moderate wear. In one specimen, LACM 124111, the anteroconid is isolated from the protoconid-metaconid complex (Fig.

Table 1. Measurements in mm of *Sigmodon lindsayi* dentition. The mean, number of specimens (parentheses) and observed range (below, parentheses) is provided for each tooth by zone. An asterisk indicates either absence of specimens or lack of observed range for single specimens. Ht = height, L = length, Occl = occlusal, W = width.

		Lower molars								
		M_1			M_2			M_3		
Zone	Crown Ht	Occl L	Basal L	Occl W	Occl L	Basal L	Occl W	Occl L	Basal L	Occl W
58.8	*	*	*	*	1.85 (1)	1.91 (1)	2.05 (2)	1.78 (1)	2.09 (1)	1.94 (1)
	*	*	*	*	*	*	(2.03–2.07)	*	*	*
57.7	1.22 (1)	*	*	2.00 (1)	*	*	*	2.25 (1)	2.60 (1)	2.04 (1)
	*	*	*	*	*	*	*	*	*	*
57.6	1.22 (8)	2.46 (12)	2.88 (12)	1.83 (11)	1.90 (4)	2.25 (3)	2.16 (4)	1.87 (7)	2.33 (7)	2.01 (6)
	(0.97–1.43)	(2.15–2.74)	(2.42–3.10)	(1.67–1.97)	(1.72–2.05)	(1.91–2.46)	(2.06–2.31)	(1.46–2.27)	(1.94–2.51)	(1.84–2.2)
55.9	*	*	*	*	1.84 (1)	*	2.03 (1)	*	*	1.92 (1)
	*	*	*	*	*	*	*	*	*	*
55.5	1.21 (2)	2.39 (2)	2.58 (2)	1.79 (4)	1.91 (4)	2.22 (2)	2.04 (4)	1.78 (3)	2.23 (3)	1.95 (3)
	(1.14–1.28)	(2.20–2.58)	(2.44–2.71)	(1.58–2.07)	(1.70–2.09)	(2.09–2.34)	(1.94–2.17)	(1.62–1.97)	(2.13–2.32)	(1.90–1.99)
53.8	1.11 (1)	2.24 (1)	2.46 (1)	1.67 (1)	*	*	*	*	*	*
	*	*	*	*	*	*	*	*	*	*

	Upper molars								
	M^1			M^2			M^3		
Zone	Occl L	Basal L	Occl W	Occl L	Basal L	Occl W	Occl L	Basal L	Occl W
58.8	2.22 (1)	2.37 (1)	2.21 (1)	*	*	*	*	*	*
	*	*	*	*	*	*	*	*	*
57.6	2.11 (7)	2.47 (7)	2.13 (9)	1.80 (9)	2.06 (9)	2.10 (11)	1.72 (12)	1.90 (12)	1.92 (11)
	(2.02–2.24)	(2.29–2.68)	(2.00–2.34)	(1.62–1.99)	(1.73–2.55)	(1.77–2.46)	(1.54–1.97)	(1.77–2.31)	(1.66–2.06)
55.5	2.30 (4)	2.80 (4)	2.15 (3)	1.77 (4)	2.00 (2)	1.91 (3)	1.85 (2)	1.84 (1)	1.85 (3)
	(2.05–2.44)	(2.48–3.06)	(1.99–2.34)	(1.64–1.91)	(1.81–2.19)	(1.83–2.03)	(1.80–1.89)	*	(1.75–1.97)

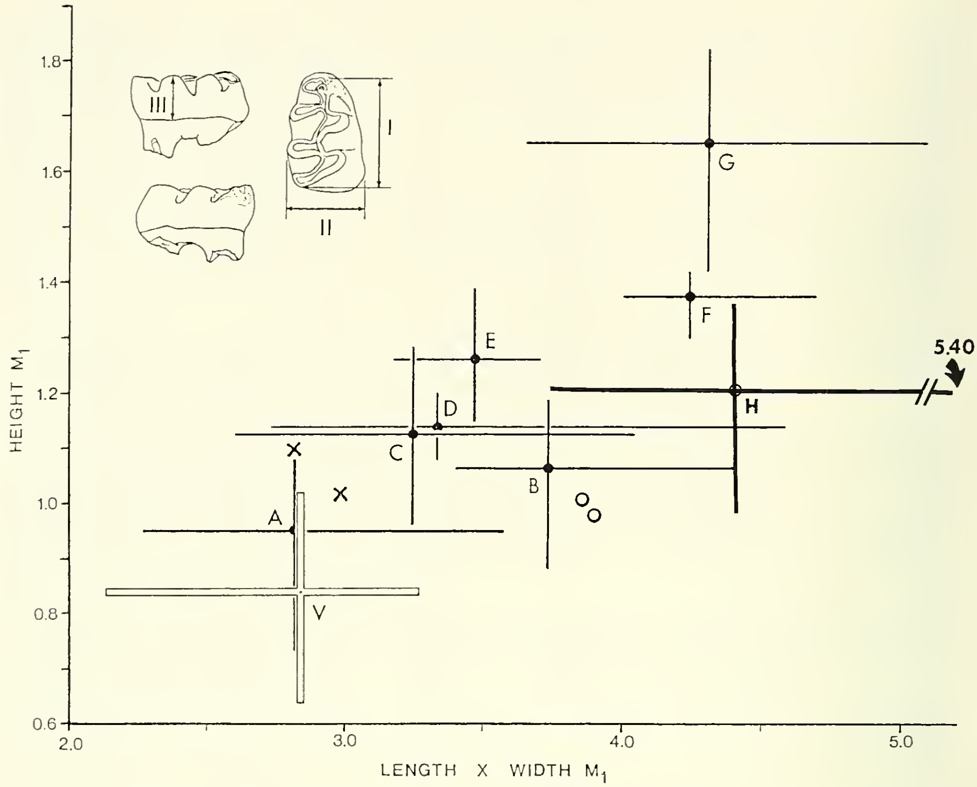

Fig. 2. Crown height (mm) of the first lower molar as a function of occlusal area (mm^2) in *Sigmodon* and *Prosigmodon* species (modified from Martin 1979 and Czaplewski 1987). Inset shows method of taking measurements: I = occlusal length, II = occlusal width, III = crown height at metaconid. V = *S. minor medius* (Verde Formation), A = *S. minor medius,* Rexroad Loc. 3, B = *S. curtisi,* Inglis IA. C = *S. libitinus, Haile* XVIA, D = *S. bakeri,* Coleman IIA, E = *S. ochrognathus* (extant), F = *S. leucotis* (extant), G = *S. hispidus,* (Reddick IA), H = *S. lindsayi,* Vallecito Creek. Horizontal and vertical lines represent the observed ranges of both measures as they pass through the grand mean. Open circles = *Prosigmodon holocuspis,* x = *P. chihuahuensis.*

3). This is unusual, but it is also occasionally expressed in teeth of extant cotton rat species.

The first lower molar of *S. lindsayi* has either three or four roots. The labial root is well developed, but the lingual root may be absent. Five of eight specimens in which the root pattern could be determined had three roots, the others four.

The single first lower molar from zone 53.8 (LACM 122964) is similar to *S. lindsayi* in size and overall morphology, but two features set this particular specimen apart from those typical for the species. First, the anteroconid, although large and somewhat laterally expanded, is not developed in this regard to the extent as in those from zone 57.6. Secondly, the tooth has only a tiny third (labial) accessory root. This is in contrast to the teeth in zones above 53.8, in which at least three, and occasionally four roots are well developed. It is only provisionally referred to *S. lindsayi.*

Additionally, in one very lightly worn M_1 from zone 55.5 (LACM 124238)

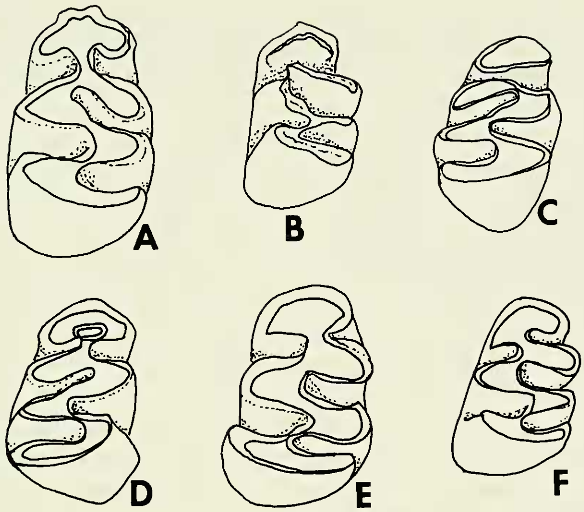

Fig. 3. First lower molars of *Sigmodon lindsayi,* new species, and *S. mascotensis. S. lindsayi*: A, LACM 124161, holotype LM_1, ×19.2; B, LACM 124124, unworn, possibly embryonic LM_1, ×16.9; C, LACM 124111, RM_1 with slightly eroded anteroconid-notice separation of metaconid from anteroconid, ×17.0; D, LACM 124117 RM_1, ×18.6; E, LACM 124123 LM_1, heavily worn, ×18.6. *S. mascotensis*: F, MSU 12531, LM_1, from a female, collected 6 mi. W Autlan, 4400 ft, Jalisco, Mexico, ×15.0.

LRA2 is more perpendicular to the midline of the tooth and the tip of the metaconid does not, as a result, appear to extend posteriorly. This may be a function of wear or it could represent a slight morphological change within *S. lindsayi* populations through time.

M_2-M_3: These teeth do not differ in any appreciable way from those of most cotton rats, such as *S. curtisi* nd *S. hispidus.* Reentrant folds are relatively deep and narrow, and the anterior cingulum is moderately to well developed on both teeth, as it is in all cotton rats except *S. bakeri* and *S. peruanus* (Martin 1979).

M^1-M^2-M^3: Likewise, the upper dentition is not diagnostic. These teeth are relatively large (Table 1), but demonstrate no specific characters which would allow separation from other middle Pleistocene species, such as *S. curtisi* or *S. hudspethensis.*

Comparisons.—*Sigmodon lindsayi* was approximately the size of *S. curtisi* (Martin 1979, 1986). Utilizing Martin's (1984) formula for estimating body mass in cricetine rodents from M_1 length, *S. lindsayi* averaged 76.6 g, with a range of 55.9–116.2 g. Occlusal length was used for these calculations.

The enlarged, symmetrically flattened and laterally extended anteroconid on M_1 is a feature that we have seen only on one specimen of the extant *Sigmodon mascotensis,* the Jaliscan cotton rat. The M_1 of MSU 12531, from Jalisco, Mexico, shows a great deal of similarity to the holotype of *S. lindsayi* (Fig. 3). However, the anteroconid is not as greatly extended laterally in two other specimens available for study. A fourth specimen of *S. mascotensis,* with the anterior portion of M_1 broken off, could be added to the analysis for a study of root count. Four well-developed roots are present on all specimens. This is in contrast to the condition in *S. lindsayi,* in which three roots are present in more than half the specimens.

An enamel atoll appears on the anteroconid of other cotton rat species, but is generally rare. We have not, in any case, seen it developed to the same extent in any other species as it was in the two specimens of *S. lindsayi.*

Discussion

Sigmodon lindsayi is an extinct member, along with *S. curtisi, S. hudspethensis* and *S. libitinus,* of the *leucotis* species group of cotton rats (see Martin 1979, 1986 for details of taxonomy), characterized by only three or a combination of three and four roots on the first lower molar. All extant cotton rats in North America except *S. leucotis* have four well-developed roots on M_1 and are members of the *hispidus* species group. Species exclusively with four roots on M_1 are first seen in the fossil record during the late middle Pleistocene. The evidence suggests that the four-rooted M_1 evolved from the three-rooted form.

The teeth of *S. lindsayi* are more high crowned than other extinct members of the *leucotis* species group (Table 1; Fig. 2). Coupled with the high percentage of first lower molars having four roots, it is conceivable that *S. lindsayi* was close to the *hispidus* species grade of dental evolution.

One of the more interesting questions is whether or not the *hispidus* species group evolved from a single common ancestor of the *leucotis* group, or if *hispidus* species group members evolved independently from two or more *leucotis* group species. If the latter, then it may be that *S. lindsayi* is ancestral to *S. mascotensis.*

Specimen LACM 122964, a lower right M_1 from zone 53.8, which we have tentatively referred to *S. lindsayi,* deserves further comment. It is, unfortunately, the only cotton rat specimen recovered from zone 53.8. Zone 53.8 occurs at approximately the 610 meter level in the Vallecito-Fish Creek sequence, well within the Vallecito Creek faunal zone. Zone 55.5, the next overlying interval which contains *S. lindsayi,* is at about the 427 meter level. We do not know how much time occurred during those 183 meters of sedimentation, because there is some doubt about the entire duration of the Vallecito Creek interval (Opdyke et al. 1977). However, if further collecting confirms the dental characters of the cotton rat at zone 53.8, then it may be that this zone represents the transition from a smaller, more generalized species such as *S. minor* to a member of the *leucotis* species group. In size and hypsodonty, LACM 122964 is similar to small specimens of *S. lindsayi* from higher zones. It is for this reason that we provisonally refer the specimen to the latter species. However, accessory roots are minimally developed on M_1, as in *S. minor,* and the anteroconid of M_1 is also not as exaggerated as it is in typical *S. lindsayi* first lower molars.

We will present a detailed analysis of morphometric change in cotton rat dentitions from the Anza-Borrego sequence elsewhere, but it is interesting to note that *Sigmodon minor,* which is ubiquitous through more than 3048 meters of sediment representing 2.0 million years prior to the first appearance of *S. lindsayi,* is not simply replaced by the latter species during the time represented by the Vallecito Creek sediments. *Sigmodon lindsayi* appears at zone 55.5 (or 53.8), and persists through zone 57.7, but it then is absent from zone 57.8, at which level only *S. minor* is encountered (14 isolated teeth and one mandibular fragment with M_1-M_3). At the next highest level, zone 58.8, *S. lindsayi* occurs once again, without *S. minor.*

Although we have no inherent reason to doubt the stratigraphic data associated with the specimens that we have studied, the pattern above has not been recorded from other depositional basins in North America, and we are suspicious that the *S. minor* specimens at zone 57.8 may belong to a lower unit. However, if this is not the case, then the pattern can be explained easily by a combination of competition and climatic modification. Martin (1986) summarized the research on competition among living cotton rats and their arvicolid analogues, and noted that one species of cotton rat rarely tolerates the presence of another *Sigmodon* or *Microtus* species, especially if it is small. Those small cotton rats that have evolved are now extinct, including *S. minor*. Therefore, it seems likely that as populations of *S. lindsayi* became established in the Anza-Borrego area, those of *S. minor* diminished. Zone 57.8 could represent a limited area in which *S. lindsayi* became locally extinct due to an unknown climatic event, allowing *S. minor* to return temporarily. At the periphery of their ranges in Kansas, an interplay of this sort occurs between *Sigmodon hispidus* and *Microtus ochrogaster* (Martin 1986). When winters are cold, populations of *S. hispidus* die off, allowing *M. ochrogaster* to repopulate the area. However, because *S. hispidus* is the more dominant species, wherever they are sympatric, *S. hispidus* generally replaces *M. ochrogaster*.

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